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LIFE HISTORY AND DESCRIPTION OF *DASINEURA GLEDITCHIAE* (DIPTERA: CECIDOMYIIDAE) IN CALIFORNIA

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Abstract.—The biology of *Dasineura gleditchiae* (Osten Sacken) (Diptera: Cecidomyiidae) was studied in California on honeylocust trees, *Gleditsia triacanthos* L. First appearance of the gall midge, documented by the capture of adults in emergence traps placed under *G. triacanthos,* was in mid-February 1996. Opaque-white, ovoid eggs with a mean (± 1 SE) length of 0.36 ± 0.006 mm were oviposited in clusters along the rachis or margins of expanding leaves. Three instars were identified; mean (± 1 SE) head capsule widths (mm) were 0.02 ± 0.001, 0.03 ± 0.001, and 0.05 ± 0.001 for the first, second, and third instars, respectively. A single first instar was found capable of initiating gall formation. Three forms of leaf galls were observed: 1) a partial fold, 2) a complete fold, and 3) a roll gall. Gall forms were found to be related to the number of larvae inhibiting galls. The mean (± 1 SE) number of larvae per gall form was 1.88 ± 0.119, 3.18 ± 0.160, and 6.88 ± 0.792, for partial, complete, and roll galls, respectively. The parasitoid and predator guild that emerged from galls containing *D. gleditchiae* included *Ceraphron* sp. (Ceraphronidae), *Lyrcus* sp. and *Mesopolobus* spp. (Pteromalidae), *Brasema* sp. (Eupelmidae), *Aprostocetus* sp. (Eulophidae) and *Orius tristicolor* (White) (Anthocoridae).

Key Words.—Insecta, *Dasineura gleditchiae, Gleditsia triacanthos,* honeylocust pod gall midge.

Thornless honeylocust trees, *Gleditsia triacanthos* L. var. *inermis* Zabel, were widely planted throughout the United States. The honeylocust tree has many desirable qualities including its purported immunity to diseases (Hepting 1971) and insect pests, adaptability to high pH and fine soil texture, heat tolerance (Graves 1994), and its availability in many attractive forms with various foliage color (Haserodt & Sydnor 1983). However, as this tree was widely planted, *Dasineura gleditchiae* (Osten Sacken), also known as the honeylocust pod gall midge, has emerged as a major pest in western United States. The cultivar 'Sunburst' is reported as the most susceptible honeylocust cultivar damaged by the gall midge (Koehler 1982). Feeding by the larvae of this cecidomyiid causes galling of the leaflets and early leaf abscission which reduces the aesthetic value of the tree (Koehler 1987).

Dasineura gleditchiae and the honeylocust tree are native to the eastern interior of the United States (Dirr 1977). The gall midge is now distributed throughout the United States and Europe (Nijveldt & Caron 1978, Del Bene 1986, Fisher & Pivot 1992). It was first documented in California in 1978 (Dowell & Gill 1989). Gall midge dispersal has presumably been through movement of infested plant material. *D. gleditchiae* is a significant pest in western United States and is rarely a problem in eastern United States.

Controlling the gall midge to protect the aesthetic value of the tree has proven difficult. Soil-applied systemic insecticides targeting the larval stage on *G. triacanthos* grown in containers (Parrella et al. 1986) and in the field (Harrigan & Saunders 1975) achieved only short term control. In addition, many of the pesticides used in these trials are restricted use materials not available to homeowners. Therefore the gall midge is able to establish on landscape trees and can then

move back into nursery stock, thus confounding control in commercial nurseries. Because of this, recommendations have been made to plant an alternative tree in California (Koehler 1987).

Much of the information reported on the biology of the gall midge is anecdotal, contains conflicts, or are generalizations which apply to the family rather than the genus. The generally accepted biology is that adult presence is first noted in the spring, oviposition begins on young, unfurled foliage from which larvae emerge. The larvae move to an appropriate feeding site (unfurled foliage), feed gregariously in the pod galls that form, and pupate within the galls (Schread 1959). Generation time has been reported to vary from 14–26 days (Del Bene 1986). The literature contains conflicts regarding what stage overwinters and where it overwinters (Schread 1959, Mayer et al. 1981, Del Bene 1986).

The limited information concerning *D. gleditchiae* probably reflects the difficulty in studying this insect. The greatest portion of the gall midge's lifecycle is spent in the larval stage which is obscured from view by gall tissue. The adults, like most cecidomyiids, are very frail and short lived.

More detailed information on the life history of *D. gleditchiae* is required to develop an IPM program for this pest. Our objectives were to describe the developmental stages, establish the number of instars, confirm the speculation that the gall midge overwinters under the canopy of *G. triacanthos,* describe gall forms, and inventory parasitoids and predators of *D. gleditchiae* in selected areas of California.

Methods and Materials

Randomly selected *G. triacanthos* L. var. *inermis* 'Sunburst' of similar age (15–20 years) with trunk diameters at a 1.2 m height of 21.0–30.0 cm, and a canopy dripline radii 5.5–8.5 m were used for the experiments unless reported otherwise. These trees were located in Davis, California.

Field Studies.—Three, 30-cm long terminals were randomly selected from two trees at each of two locations (12 terminals total) one time, during May 1995. Eggs were removed from the terminals using a moistened camel hair brush, immediately placed on slides, and kept moist with 70% ethyl alcohol. Larvae and pupae were removed from galls with the aid of fine tipped probes, immediately placed on slides, and kept moist with 70% ethyl alcohol. All life stages were measured and photographed using a Wild® photomacroscope at 50× magnification.

Additional pupae were removed from galled plant material and placed in petri dishes with moistened filter paper. These were then placed in an environmental chamber set at 26° C, 60% RH, 12:12 (L:D). Pupae were checked daily for color change until adults emerged which were then sexed. Observations were conducted to see if sexual dimorphism was apparent in the pupal stage.

Greenhouse Study.—Newly emerged adults (approximately 12 h old) were taken from emergence cages containing galled foliage. Adults were confined in clip cages attached to unexpanded foliage of containerized trees in a greenhouse. Clip cages were distributed over ten trees with three cages per tree, each on a separate branch. Clip cages were monitored every 2 h until egg deposition (4 h total) was first observed. Clip cages and the adults were then removed. Monitoring of egg hatch through adult emergence was done using a 10× hand lens and by

destructive sampling for viewing under a dissecting microscope. Observations were conducted at 12 h intervals from the time of removal of the clip cages until adult emergence. All life stages were observed for purposes of description and biology.

Clip cages were made of clear 2.5 cm acrylic tubing which had been cut into 2.5 cm lengths. Ventilation was provided through nylon chiffon material that was hot-glued over one end. A pipe cleaner was hot-glued onto the circumference of the end which was placed in contact with the foliage. With the open end of the cage facing down, the acrylic cage was hot-glued to the upper arm of a hair clip which was bent in a 90° angle. Then a 3.0 cm square of adhesive-backed foam weather stripping was hot-glued to the lower arm of the hair clip. A leaf lamina was placed between the clip cage and the foam weather stripping. The foam provided rigidity resulting in a better seal to prevent escape of the adult gall midges.

Instars.—The number of instars was determined using Dyar's Rule (Dyar 1890). Larvae were placed in 70% ethyl alcohol on slides for measuring head capsule width and body length and width using a microscope fitted with an ocular micrometer. Head capsule data were statistically analyzed using Cluster Analysis (SAS Institute 1994). The relationship between body length (dependent variable) and head capsule (independent variable) was analyzed using linear regression (SAS Institute 1994).

Overwintering.—Emergence traps and soil core sampling were used to confirm that the soil below the canopy of honeylocust trees was an overwintering site of *D. gleditchiae.* Emergence traps were made of inverted, white, three-gallon plastic buckets; each covered 452-cm^2 area of ground surface. Five-cm diameter ventilation holes were cut into the vertical sides of the buckets and covered with organdy material. A 50 ml centrifuge tube was hot-glued to the top of each bucket to collect emerging adults.

Beginning January 1996 emergence traps were placed under randomly selected trees from each of three sites. The ground surface under the tree canopies differed between sites: Site 1) unmaintained grasses; Site 2) no vegetation because of the use of herbicides; Site 3) mowed grasses.

At each site 30 emergence traps were placed within the drip line of a honeylocust tree. Collection tubes were removed and capped every four days from January to mid-April 1996. Tubes were taken to the laboratory where positively identified *D. gleditchiae* adults were counted and sexed.

Soil cores, 5.0 cm diameter wide by 7.0 cm depth, were collected during February 1996. Randomly selected trees from each of four sites in Davis, California were used. The surface treatment, mowed grasses to within approximately 30.0 cm of the base of the tree trunks, was the same at each site.

Soil cores were collected from 37.5, 150.0 and 300.0 cm from the base of honeylocust trees. The soil cores were placed in sealed bags and returned to the laboratory. Each soil core was placed in a brine solution. Floating cocoons were removed from the solution and placed in petri dishes with moistened blotters in an environmental chamber with a mean temperature of 26° C, 40% RH, 12:12 (L:D) until adult arthropods emerged. Voucher specimens of emergent material were deposited in the Bohart Museum of Entomology, University of California, Davis.

Tree Phenology and Gall Form.—At five day intervals during March 1996, bud expansion was monitored by collecting ten outer canopy terminal branches with a minimum of ten buds. A rating system for bud expansion was devised in which 1 = bud scales tight, no green vegetation visible with an unassisted eye and 2 = green vegetation showing the beginning of bud expansion.

Gall forms were assayed by sampling from two sites. Galls were rated as 1) partial fold, 2) complete fold, or 3) roll gall; the designation of fold gall was determined using Russo's terminology (1979). The number of larvae within each form was also recorded.

The minimum number of larvae required to initiate a gall and the earliest instar that can initiate a gall was determined. At 20 h after observation of eclosion first instars (n = 4) that were solitary on four, individual, unexpanded leaflets, were removed from the leaflets. Those four leaflets, left attached, were monitored daily for 14 d at which time galling characteristics of the leaflets were observable.

Parasite/Predator Observations.—We evaluated the natural enemy complex associated with *D. gleditchiae* in six Californian counties (Yolo, Sacramento, Tulare, Fresno, Stanislaus, Madera) covering a distance of 402 km north to south. 1) Fifty terminals were collected (once every three weeks from April to June 1995) from honeylocust trees in each of the six counties. The terminals were placed in emergence buckets after visual inspection to assure that the terminals were free of other pests. Emergence buckets were taken to the laboratory and inspected periodically for emergence and identification of natural enemies. 2) In Yolo county additional observations were conducted by 2 methods: A) Every 2 weeks twenty pinnules with varying numbers of galls were collected at a height of 1.0–5.5 m from a honeylocust tree in mowed grass. A total of 160 pinnules were collected. Collecting began at the first appearance of galling (late April) and continued until galling was no longer apparent (late July). Petri dishes containing the samples were placed in an environmental chamber with a temperature of 26° C, 60% RH, 12:12 (L:D). B) Gall midge cocoons, collected from soil core samples using a brine flotation technique, were placed in an environmental chamber with a mean temperature of 26° C, 40% RH, 12:12 (L:D). Emergent arthropods were collected and identified. Voucher specimens of emergent material were deposited in the Bohart Museum of Entomology, University of California, Davis and the USDA, Systematic Entomology Laboratory, Beltsville, Maryland.

Results

Eggs.—(Fig. 1A and Table 1). Eggs were elongate-ovoid and newly deposited eggs were opaque-white which progressed to opaque-red at eclosion. A red spot was observed in each egg as the embryos matured. Eggs were laid singly or in clusters along rachis or marginal folds of unexpanded leaflets. Eggs could be

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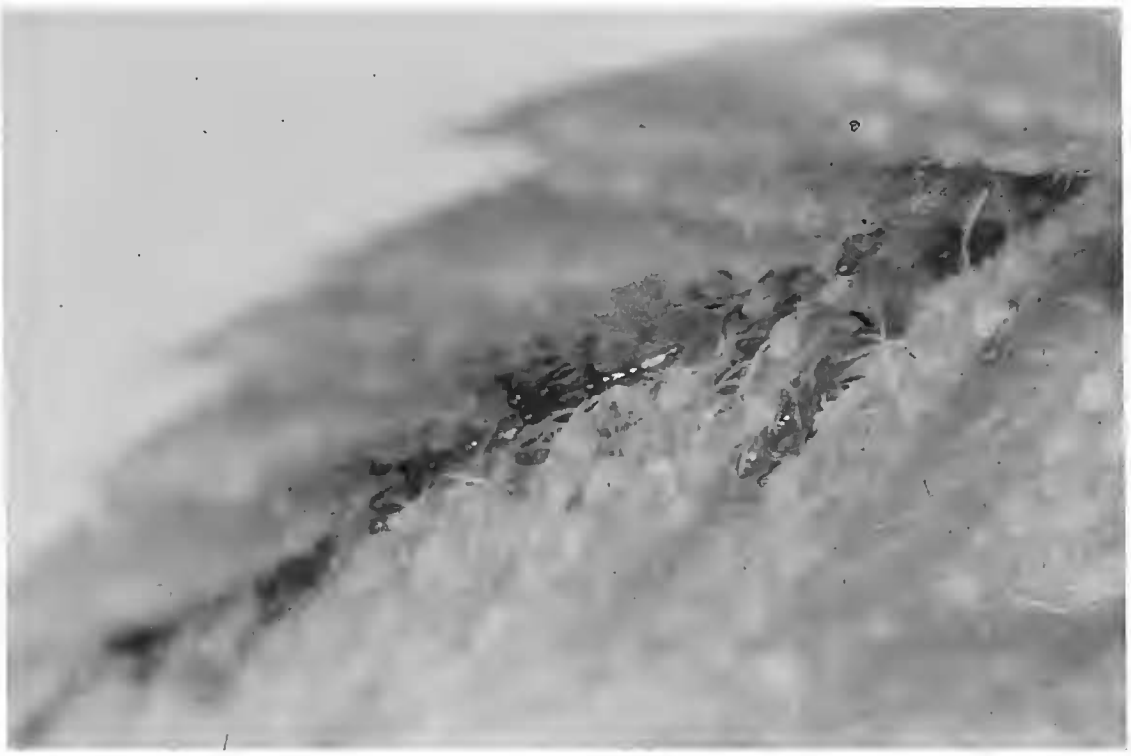
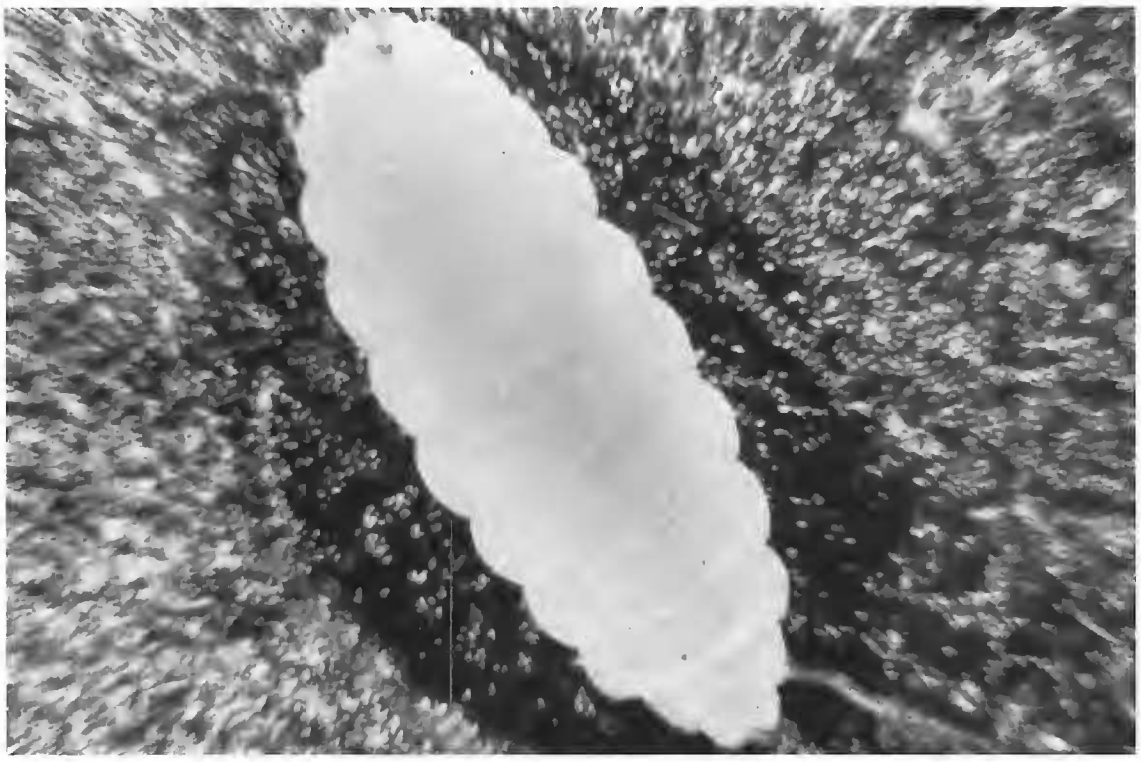
Figure 1. Photographs of various stages and damage. (A) cluster of eggs along rachis of unexpanded leaflets; (B) first instar; (C) second instar; (D) third instar; (E) various color phases of pupae; (F) adult male *D. gleditchiae*; (G) undamaged compound host leaf; (H) galled leaf; (I) exuvium protruding from gall with newly emerged adult.





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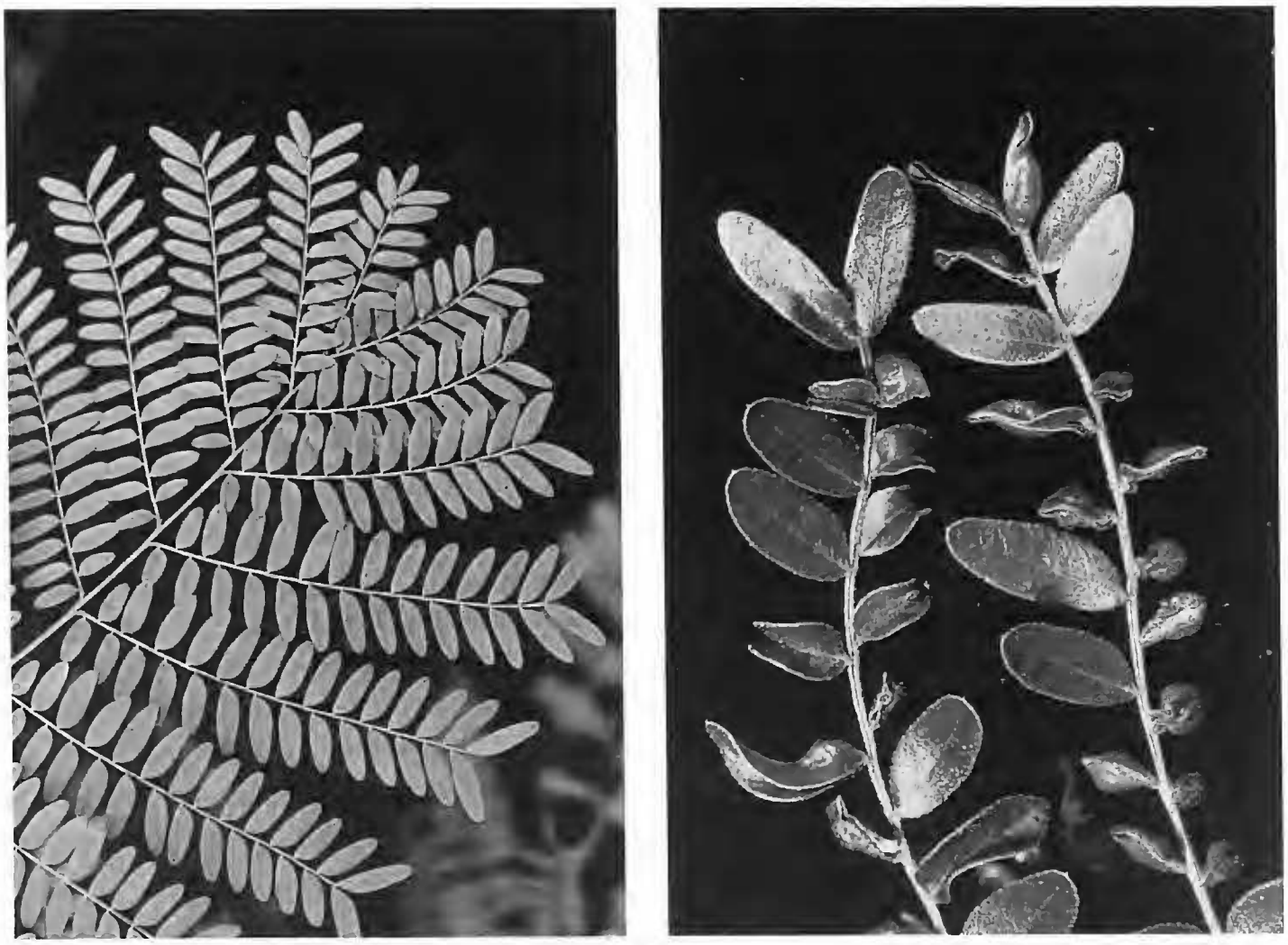

Figure 1. Continued.

Table 1. Descriptive data on the life stages of *Dasineura gleditchiae.*

Life stage	*n*	Mean ± 1 SE (mm)		
		Length	Width	Head capsule width
Egg[a]	96	0.36 ± 0.006	0.10 ± 0.002	—
First instar[b]	20	0.57 ± 0.034	0.14 ± 0.001	0.02 ± 0.001
Second instar[b]	61	1.49 ± 0.089	0.35 ± 0.024	0.03 ± 0.001
Third instar[b]	26	2.44 ± 0.108	0.57 ± 0.024	0.05 ± 0.001
Pupa[c]	29	2.43 ± 0.042	0.84 ± 0.017	—
Adult female[d]	15	1.85 ± 0.056	0.53 ± 0.026	—
Adult male[d]	3	1.79 ± 0.064	0.49 ± 0.052	—

[a] = Length measured from apical to distal most end; width measured at medial point.

[b] = Length measured from apical end of extended head capsule to distal end of the abdomen; width measured at third segment of the abdomen.

[c] = Length measured from apical end of head to distal end of the abdomen; width measured at third segment of the abdomen.

[d] = Length measured from apical end of head to distal end of the ninth abdominal segment; width measured at third segment of the abdomen; there was no significant difference analyzed by Student *t*-test ($P < 0.05$) between the measurements of adult females and males.

easily confused with similarly shaped and colored trichomes also present at this location on the leaflets.

Instars.—(Figs. 1B–D and Table 1). Newly hatched instars contained a red spot at the anterior end. First instars were cylindrical, opaque to white, and had a smooth integument with annular rings. Second and third instars were elongate and dorso-ventrally flattened. The body consisted of a head, three thoracic, and nine abdominal segments. Color varied from white to orange and heads were small and retractable with two-part antennae. The integument progressed from smooth to pebbled as later instars developed. The instar lengths ranged from 0.57 mm in the first instar to 2.44 mm in the third instar.

The third instar bilobed spatula or "breast bone" was observed through the second instar integument on the prothorasic venter. The spatula became more apparent as the second instar integument was shed.

Pupae.—(Fig. 1E and Table 1). Pupae, approximately 2.43 mm long, were obtect with horn-like spines located at the base of the antennae. Color was white at early development but progressed to light orange or red at eclosion. Pupae were sexually dimorphic; females had a red abdomen whereas the males had a gray abdomen.

Adults.—(Fig. 1F and Table 1). Antennae were long and moniliform with 12 flagellar segments. No ocelli were present and the compound eyes were of the holoptic type. Wing venation was reduced with the costal vein ending before the wing tip and the subcostal vein approximately ½ the length of the costal vein. The thorax was gray with two prominent black, longitudinal stripes. Tarsomere one, of a total of five, was considerably shorter than tarsomere two and the tarsal claws had large, basal teeth.

Adult flies were sexually dimorphic. Males had a gray abdomen and stalks on the flagellomeres of the antennae. Antennae of the males were longer than antennae of the females. Females had red abdomens and lacked the flagellomere stalks. Female body length (Student *t*-test; $t = 0.431$, df = 16, $P = 0.05$) and width

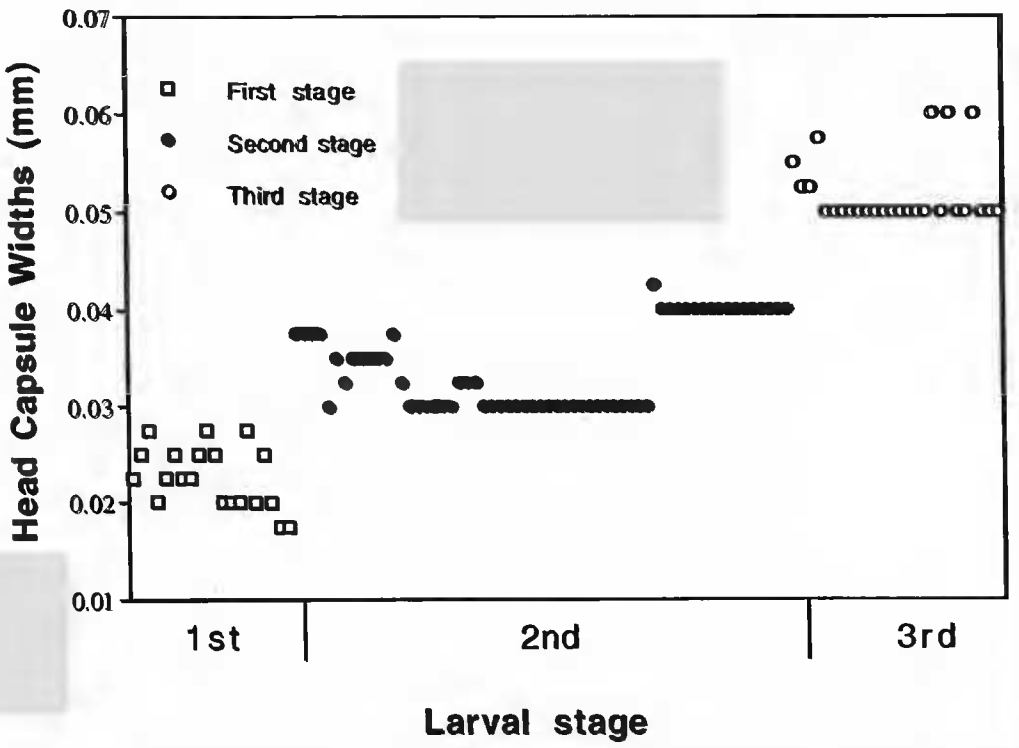

Figure 2. Clustering of head capsule widths distinguishing instars of *D. gleditchiae.*

(Student *t*-test; $t = 0.598$, df = 16, $P = 0.05$) was not significantly greater than the male. The terminal abdominal segment of the female consisted of a protrusible ovipositor whereas for the male the terminal segment was formed into a clasper.

Biological Observations.—At a mean (± 1 SE) temperature of 29 ± 1.33° C egg eclosion began 44 h after oviposition. First instars traveled by an undulating motion to a feeding site; the adaxial side of a leaflet lamina. A single, first instar was found capable of gall initiation. All instars fed within galls. Pupation was observed to occur in galls or within silken cocoons in the soil.

Just before adult eclosion from pupae in galls, pupae extended one-half their anterior length between the leaflet folds that created the galls. Adults (Fig. 1I) emerged from "T"-shaped slits formed on the dorsal side of the pupal exuviae, which remained extended between the leaf folds after emergence. Third instars of later generations fell from the galls to the soil and traveled by undulating motions to locations that provided shelter from sunlight. Soil cores taken in the spring contained cocoons with third instars or pupae in them. Duration of the larval and pupal stages at 29 ± 1.33° C ranged 14–21 and 3–5 d, respectively.

After July 1995 and 1996, no eggs were observed. The honeylocust trees continued to produce new foliage until late September when leaves began to abscise.

Instars.—Cluster analysis, based on head capsule widths, indicated three instars (Fig. 2). Head capsule widths progressed within the expected geometric ratios (Dyar 1890); a 1.5 ratio between the first (0.02 mm ±) and second (0.03 mm ±) instar and a 1.6 ratio between the second and third (0.05 mm ±) instar.

Overwintering.—(Fig. 3). Two of the three sites had very few captures. We only present data from one collection site—Site 3. Site 3 captures occurred over a 56 day period; beginning mid-February and ending mid-April with peak emergence mid-March. Adult gall midges were captured in emergence traps prior to noticeable bud expansion of the honeylocust trees, suggesting partial asynchrony between adult emergence and availability of oviposition sites.

Gall Description.—(Table 2). Newly formed galls were green or reddish in color and older, empty galls turned brown and abscised. Three forms of leaf galls

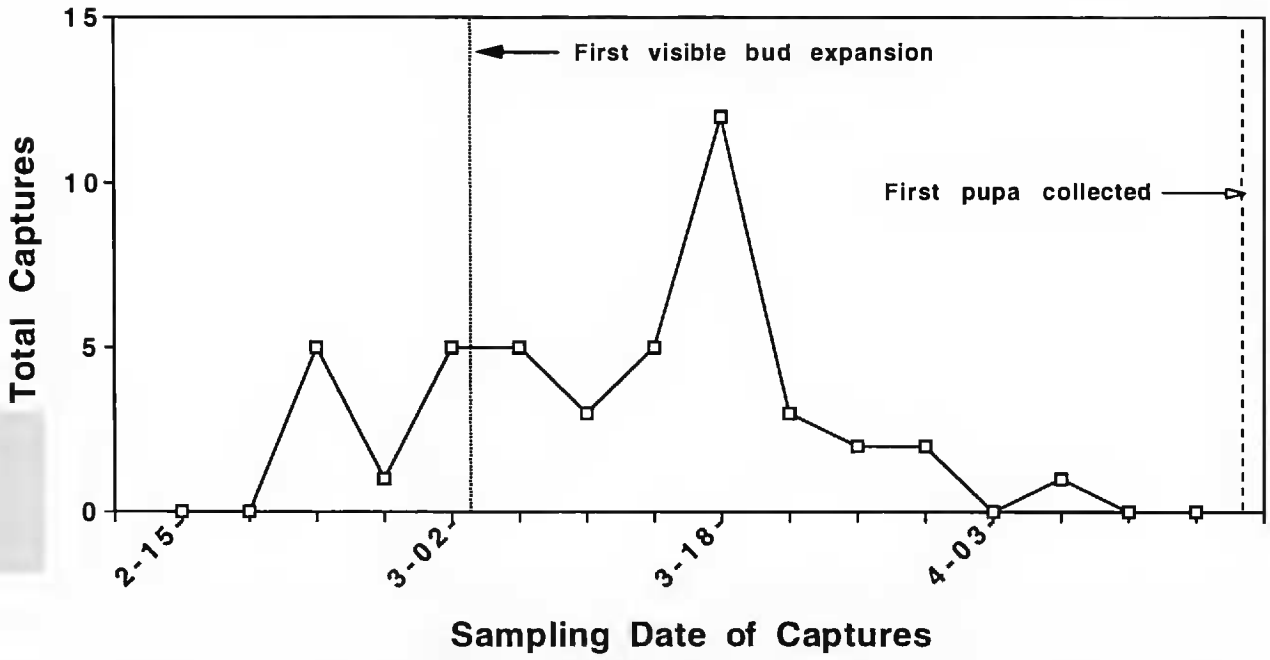

Figure 3. Total capture of adult *D. gleditchiae* in emergence traps during 1996. Buds on honeylocust trees did not begin noticeable expansion until early March. First pupa collected from tree foliage in late April.

were observed; a partial fold—less than 50% of a leaflet forms the gall, a complete fold—the complete leaflet forms the gall, and a roll gall—the leaflet margins curl on the adaxial side towards the midvein. There were significant differences between the mean number of larvae in the gall forms; a partial fold contained an average of 1.88 larvae, the complete fold contained an average of 3.18 larvae, and a rolled gall contained an average of 6.88 larvae. During the study, the most common type of gall observed was the complete fold.

Predator/Parasitoid Observations.—(Table 3). Generalist feeders collected in association with the gall midges and the honeylocust trees included Araneida, Coleoptera, Hymenoptera, and Hemiptera. One generalist predator, *Orius tristicolor* (White), emerged from a gall.

The majority of the parasitoids, eulophids and pteromalids, did not begin to emerge until mid-April. The number of parasitoids increased over time, peaking in early June and declining in July. All the parasitoids appeared to be larval/pupal parasitoids. Of the emerged parasitoids, 95% of them were pteromalids. A *Ceraphron* sp. (Ceraphronidae), typically associated with soil-dwelling arthropods, emerged in mid-February from one cocoon extracted from a soil core sample.

Table 2. Number of *Dasineura gleditchiae* larvae found in different gall forms.

Gall form	Mean ± 1 SE[1]	*n*	Range	
			Low	High
Partial	1.88 ± 0.120a	136	1	9
Complete	3.18 ± 0.160b	379	1	23
Roll	6.88 ± 0.792c	41	1	21

[1] Means followed by a different letter are significantly different (single factor ANOVA; $F = 44.0$; $df = 2, 553$), using Tukey's mean separation test ($P \leq 0.001$).

Table 3. Arthropods reared from honeylocust galls collected in California.

Family	County	Genus	Species
Anthocoridae	Yolo	*Orius*	*tristicolor*
Ceraphronidae	Yolo	*Ceraphron*	sp.
Eulophidae	Yolo	*Aprostocetus*	spp.
Eulophidae	Sacramento	*Aprostocetus*	spp.
Eupelmidae	Stanislaus	*Brasema*	sp.
Pteromalidae	Yolo	*Lyrcus*	sp.
Pteromalidae	Stanislaus	*Lyrcus*	sp.
Pteromalidae	Sacramento	*Lyrcus*	sp.
Pteromalidae	Yolo	*Mesopolobus*	spp.
Pteromalidae	Tulare	*Mesopolobus*	sp.

Discussion

Along the rachis surface and the margins of unexpanded leaflets are trichomes of a similar length and width as an egg of *D. gleditchiae.* The eggs oviposited amongst trichomes are cryptic, as evidenced by the difficulty in distinguishing eggs from trichomes without high magnification or experience. The cryptic nature of the eggs may protect them from predation.

Egg length in California was similar to that in Italy (Del Bene 1986). However, our findings differed from those of Schread (1959) and Mayer et al. (1981) who reported kidney shaped eggs of a lemon-yellow to amber color. This variation in color may be due to different species or subspecies which occur in other areas or it may simply be subjective.

The presence of a spatula has been used to identify the last instar in other cecidomyiids (Pitcher 1955, Wilson 1966). However, if the spatula is not observed under the second instar integument of a *D. gleditchiae,* a third instar may be misidentified as a second instar. Casual observation alone is not adequate for instar determination.

Pupal sex can be determined by the color of the abdomen. *Dasineura* females are proovigenic and eggs within the abdomen give pupae a red appearance. When eggs are removed from the abdomen the color changes to gray and resembles a male abdomen. Abdominal color in late pupal stages can be used to distinguish sex and could be useful in demographic analyses for determining sex ratios, sexual survivorship, and projecting population growth.

Horns on the anterior end of the pupae are present on *D. gleditchiae* and many other cecidomyiid genera. Gagné (1989) believes they function in aiding pupal escape from cocoons or galls. Our observations support this. The folds of galls must be pried apart in order for the pupae to extend out for adult emergence. The horns appear to be the only sclerotized parts of the pupae capable of serving this function.

The adults in this study were <2.00 mm long, which was considerably smaller than those from Washington which were about 3.0 mm long (Mayer et al. 1981). This size discrepancy remains unexplained.

Descriptive characteristics measured for adults in this study agree with those given by Osten Saken (1866), who originally described the gall midge from Rhode

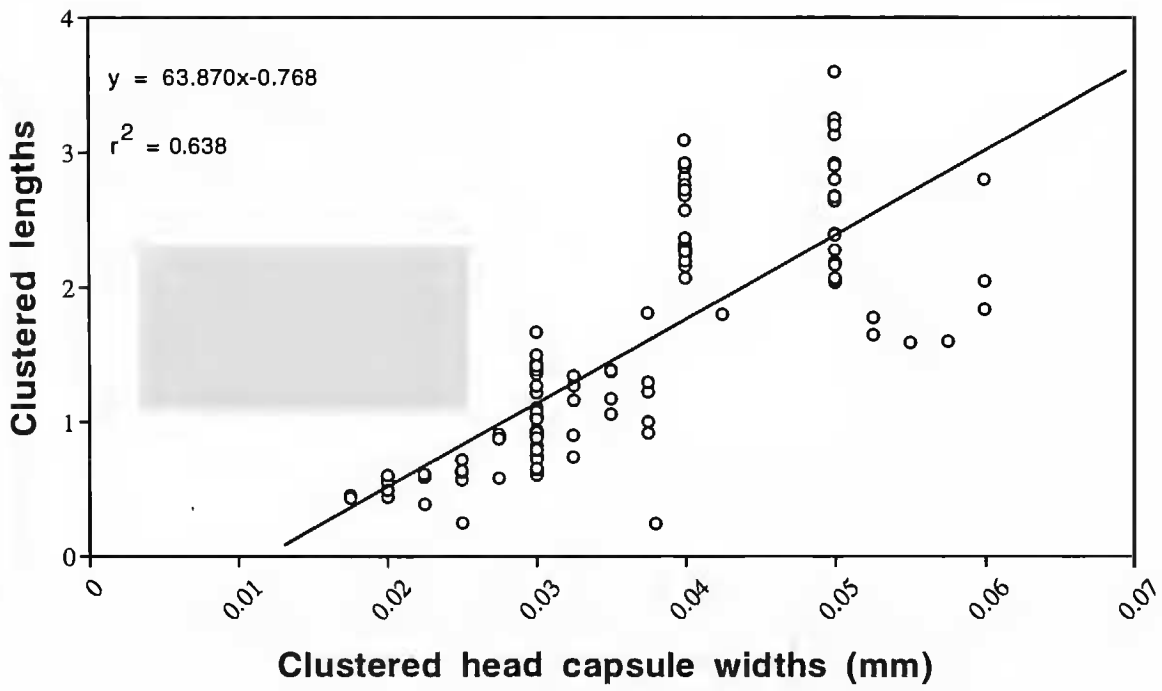

Figure 4. Correlation between length (dependent variable) and the head capsule widths (independent variable).

Island. A more detailed description of adult morphology is discussed in the Manual of Nearctic Diptera (Gagné 1981).

Gagné (1989) stated that cecidomyiids have three instars and our measurements of head capsule widths distinguish three distinctive instars for this species (Fig. 2). Instar length was less discrete than head capsule widths. Length can be used to classify instars but it is more variable and less reliable than head capsule widths as a predictor of instar (Fig. 4).

Emergence of *D. gleditchiae* from the soil was previously undescribed. We detected emergence of adults prior to noticeable bud expansion of *G. triacanthos*. There are reports which link emergence of cecidomyiids with the first flush of growth on host plants (Mayer et al. 1981). Asynchrony of gall midge emergence and bud expansion may result in reduced gall midge densities whereas years when synchrony does occur, high gall midge densities may occur early in the season.

A factor that complicates control strategies of *D. gleditchiae* is the finding that a single first instar can initiate galling. Control strategies are usually directed at preventing gall formation to preserve the aesthetic value of landscape trees. In the landscape setting, typically there is no tolerance of pest damage.

The gall midge is a gregarious feeder. We observed a range of 1–33 larvae per gall. Del Bene (1986) reported a range of 1–8 larvae per gall in Italy. Osten Saken (1866) described two gall forms initiated by *D. gleditchiae*; galls made of complete leaflets and galls made of partial leaflets. He reported 2–3 larvae per gall but did not distinguish the number of larvae per gall form. We found that leaf gall form for *D. gleditchiae* may be a function of the number of larvae initiating galling.

The results show that the mean density of larvae differs between gall forms. With this information a rapid estimate of population size may be made by observing gall forms present. This would greatly expedite monitoring of populations for making pest decisions.

Many of the same wasp families associated with *D. gleditchiae* in California, especially the Pteromalidae, were also reported from galls of *D. gleditchiae* in

Italy (Del Bene 1993). The pteromalid, *Lyrcus catalpae* (Crawford), has been reared from *D. gleditchiae* in Ohio (Krombein et al. 1979) but this is not the same species found in California. In addition to the families of Hymenoptera that we reared from *D. gleditchiae* galls in California, members of the Torymidae and Platygasteridae were reared from galls of *D. gleditchiae* in Italy (Del Bene 1993). It is not possible to compare species between California and Italy because many of the parasites found in California have only been identified to genus level and appear to be new species (S. Heydon, personal communication).

Dasineura gleditchiae is not a severe pest in its native distribution which suggests that the insect is suppressed by natural enemies (Gonzalez & Gilstrap 1992). Currently, the natural enemies of *D. gleditchiae* have not been inventoried in the pest's native geographic distribution but cataloging has been initiated (K. Valley, personal communication). Once those investigations are complete, the complex can be assessed for structure, climatic suitability, and other factors to determine if members can be brought to California to attain biological control of this pest.

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